

Web decoration of *Micrathena sexpinosa* (Araneae: Araneidae): a frame-web-choice experiment with stingless bees

Dumas Gálvez¹: Smithsonian Tropical Research Institute, Roosevelt Avenue, Tupper Building – 401, Balboa, Ancón, Panamá, República de Panamá. E-mail: dumas.galvez@unil.ch

Abstract. The function of silk web decorations in orb weaving spiders has been debated for decades. The most accepted hypothesized functions are that web decorations 1) provide camouflage against predators, 2) are an advertisement for vertebrates to avoid web damage, or 3) increase the attraction of prey to the web. Most studies have focused on only a few genera, *Argiope* being the most common. In this study, I evaluated the prey attraction hypothesis of silk decorations for a species of a poorly studied genus in this topic, *Micrathena sexpinosa* Hahn 1822. I used a web-choice experiment in which I presented empty or web-bearing frames at the end of a tunnel to stingless bees (*Tetragonisca angustula*). This frame-choice experiment consisted of the following comparisons: decorated web vs. empty frame, decorated web vs. undecorated web, and undecorated web vs. empty frame. Webs with decoration intercepted significantly more bees than empty frames and undecorated webs. Therefore, the decorations of *Micrathena sexpinosa* might play a role in increasing foraging success.

Keywords: Decorated, foraging, stabilimenta, undecorated

A diverse number of orb weaving spiders distributed in both tropical and temperate zones add silk web decorations, or stabilimenta, to their webs (Scharff & Coddington 1997). Their function is unknown, and at least six functions have been suggested for these structures (Herberstein et al. 2000; Bruce 2006). 1) They may camouflage the spider against predators (e.g., Eberhard 2003), 2) lure prey to the web (e.g., Li et al. 2004), 3) work as advertisement to vertebrates so as to avoid web damage (e.g., Eberhard 2006), 4) stabilize the web (Bruce 2006), 5) produce shade for thermoregulation of the spider (Humphreys 1992), or 6) collect water from the dew for the spider's consumption (Walter et al. 2008). The fact that web decorations are only found in diurnal species strongly suggests a visual function (Scharff & Coddington 1997). However, other possibilities are not necessarily mutually exclusive, although evidence supporting two or more functions at the same time for any species is lacking (but see Watanabe 1999, 2000).

Studies have mostly tested putative visual functions (Herberstein et al. 2000; Bruce 2006). Evidence in favor of the two most popular hypotheses (1 and 2) is contradictory. Several studies suggest that decorations can deter the attack of a predator or camouflage the spider (e.g., Blackledge & Wenzel 2001; Eberhard 2003; Li et al. 2003; Chou et al. 2005; Gonzaga & Vasconcellos-Neto 2005), but other researchers did not find evidence in favor of an anti-predator function (Herberstein 2000; Seah & Li 2001; Bruce et al. 2001; Li & Lim 2005; Eberhard 2006; Jaffé et al. 2006; Cheng & Tso 2007). One of the criticisms against this hypothesis is that decorations can attract predators to the web as well (e.g., Bruce et al. 2001).

In contrast, the prey-attraction function suggests that decorations could resemble UV gaps in vegetation, eliciting escape behavior in flying insects, or they could imitate food resources that reflect UV, luring prey (Craig & Bernard 1990). Many researchers found that decorated webs intercept more

prey than undecorated webs (e.g., Watanabe 1999; Herberstein 2000; Bruce et al. 2001; Craig et al. 2001; Li et al. 2004; Li 2005; Bruce & Herberstein 2005; Cheng & Tso 2007), but some researchers found no evidence in favor of the hypothesis (e.g., Blackledge & Wenzel 1999; Hoesel et al. 2006; Jaffé et al. 2006; Bush et al. 2008; Eberhard 2008; Gawryszewski & Motta 2008). One shortcoming of this hypothesis is that prey could apparently detect and avoid the web by the presence of the decoration (e.g., Blackledge & Wenzel 1999).

Using stingless bees, I tested the prey-attraction hypothesis for the less well-studied *Micrathena sexpinosa* Hahn 1822. *Micrathena* is a Neotropical genus that constructs web decorations (Herberstein et al. 2000). Nevertheless, no one has tested any hypothesis regarding the function of these decorations in any of the species. In contrast to the model genus *Argiope* with its polymorphism of designs (Herberstein 2000) that perhaps correlate to several functions (Bruce & Herberstein 2005), *M. sexpinosa* consistently produce the same decoration (D. Gálvez pers. obs.), a line of silk on the top of the hub of the web (Fig. 1).

I used a trial tunnel in the field combined with decoration removal to test the preference of stingless bees for webs with decorations. In my design, prey nesting in a wooden box had to fly out of the tunnel and choose an exit in which the different web treatments were placed (Gálvez 2009). An advantage of this approach is that it mimics natural visual conditions better than laboratory experiments (Bruce 2006). I predicted that if web decorations function to attract prey, then decorated webs would intercept more bees than the undecorated webs or empty frames.

METHODS

Site & species.—I carried out these experiments at La Selva Biological Station in Heredia, Costa Rica (10°26'N, 83°59'W), a 1550-ha reserve in the Atlantic lowlands with an annual average rainfall of 4000 mm³ (Sanford et al. 1994). *Micrathena sexpinosa* is a small orb-weaving spider occurring in the tropics that constructs its web in the midst of dense vegetation, woven on a vertical plane or slightly inclined (10–20°, Newt

¹ Current address: Department of Ecology and Evolution, University of Lausanne, Biophore, UNIL-Sorge, CH-1005 Lausanne, Switzerland.



Figure 1.—Araneid *Micrathena sexspinosa* on its web eating a stingless bee. The spider rests at the center of the hole in the web; the decoration is built next to it. The arrow indicates part of the decoration. Scale bar = 1 cm.

1985), with a central hole through which the spider can move easily from one side to the other (Nentwig et al. 1993). Next to this hole, the spider usually builds a linear decoration like other *Micrathena* species (Herberstein et al. 2000). I identified the spiders using Levi (1985).

Experimental apparatus and treatments.—Without being systematic, I collected samples of *M. sexspinosa* and their webs daily from the field (around buildings and greenhouses) by sticking the webs to cardboard frames (18 × 18 cm), with a hole in the middle (324 cm²). The side of the frame used to bear the web had adhesive tape placed with the sticky side facing the web. This tape was fixed to the frame by wrapping it to the corners of the frame with adhesive tape. I removed decorations from 16 out of 34 webs by burning the silk with a heated fine-pointed forceps while the spider was still on the web. In case some damage was done to the web during the burning process, particularly to the sticky spirals, I used the forceps to damage a similar area of the orb on the decorated web to be used for comparison. I collected a total of 34 spiders and used only one orb from each spider.

I placed the webs at the end of a 300 × 120 × 80 cm tunnel (Fig. 2), open at both exits, modified from Gálvez (2009). Since the frames did not match the area at the end of the tunnel, the remaining spaces were covered with cardboard. I placed a wooden box (40 × 30 × 20 cm) with a nest of the stingless bee *Tetragonisca angustula* Latreille 1811 at one of the ends of the tunnel. Thus the bees could fly out of the tunnel through either the end bearing the frames (A in Fig. 2) or the end next to the nest (B in Fig. 2); however, bees flew in or out always through the end bearing the frames (during the trials). I placed the nest in the tunnel with both exits opened for 48 h before the beginning of the experiments in order to get the bees acclimated to the tunnel and the new nest location.

I carried out a two-frame choice experiment in which the bees were exposed to two frames placed at the same end of the

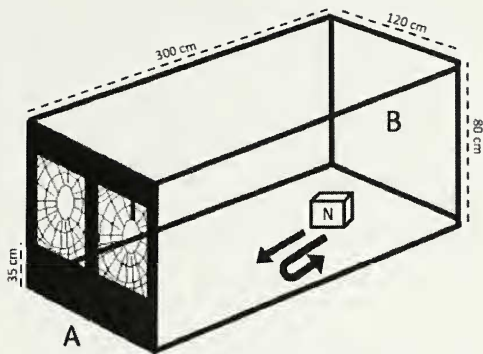


Figure 2.—Trial tunnel in which the *Tetragonisca angustula* stingless bees were exposed to the different web treatments of *Micrathena sexspinosa*. The walls and roof of the tunnel are not shown in order to reveal the interior. Both exits of the tunnel were opened (A and B); therefore bees could fly out of the tunnel from the nest (N) by either exit (arrows). See text for details about the frames bearing the webs. This figure depicts the comparison between a decorated (A right) and an undecorated web (A left).

tunnel. Three variations of the choice experiment were performed: “decorated web vs. empty frame” ($n = 8$ pairs, 86 bees) “decorated web vs. undecorated web” ($n = 9$ pairs, 96 bees), and “undecorated web vs. empty frame” ($n = 7$ pairs, 72 bees). I kept the spiders on the webs and used individuals of similar sizes with the intention of comparing the two web treatments. I controlled the effect of web size, since the webs for each treatment always covered the same area in the frame (324 cm²). The exit of the tunnel bearing the frames was in front of herbaceous vegetation, with a dark green mesh placed one meter from it in order to increase the contrast between the webs and the background (Bruce et al. 2005).

I counted the numbers of bees either being intercepted (including bees caught by spiders) or flying through the empty frame (hereafter referred to as “number of bees intercepted,” although the empty frames could not intercept bees). I switched the relative (left/right) positions of the frames each time two bees had exited the tunnel or were intercepted in order to avoid any possible bias due to frame position. The frames were placed at the exit of the tunnel only when no bee was leaving the nest or flying in the tunnel. In cases in which three or more bees accumulated in the web because the spider did not attack them, I removed the frames and used forceps to remove the bees in order to avoid the possibility that bees caught there would deter more bees from flying into the web. The damage to the webs using this procedure was minimal and it was not taken into account for the analysis. I did not remove the bees if they were captured by the spider or wrapped with silk by the spider (1–2 bees per trial). After this, I put the frames back at the exit to continue the experiment. I used 9–10 bees per pair of frames, which required a new pair of webs made by fresh spiders.

I tested for a significant effect of web type on the likelihood of bee interception using a linear mixed model. I treated the

Table 1.—Statistical summary and preferences for the two-frame choice experiments set for *Micrathena sexspinos*. Abbreviations: dec = decorated webs; undec = undecorated webs; empty = empty frames.

Treatment	Z	P	n	Total number of bees	% of bees intercepted		
					dec	empty	undec
dec vs. empty	3.90	< 0.001	8	86	65	35	----
undec vs. empty	0.829	0.407	7	72	----	46	54
dec vs. undec	2.74	0.006	9	95	60	----	40

counts of bees intercepted per web type in each trial as proportional data. I evaluated web type (between pair of frames) as the main effect and trial as random effect. Therefore, I carried out an analysis for each frame choice experiment. I accepted effects as statistically significant for $P \leq 0.05$, and I carried out all analyses in R 2.10.0 using the function lmer, specifying the binomial distribution for proportion data (R Development Core Team 2009).

RESULTS

In this two-frame choice experiment, I compared "decorated webs versus empty frames" for 8 pairs of frames (86 bees), "undecorated webs versus empty frames" for 7 pairs (72 bees) and 9 pairs (96 bees) for "decorated webs versus undecorated webs." Decorated webs intercepted significantly more bees (65%) than the empty frames (35%, $Z = 3.90$, $P < 0.001$, Table 1). Decorated webs intercepted more bees than undecorated webs as well (40%, $Z = 2.74$, $P = 0.006$, Table 1). I found no differences in the number of bees intercepted between undecorated webs and the empty frames ($Z = 0.829$, $P = 0.407$, Table 1).

DISCUSSION

The prey attraction hypothesis proposes that decorations may increase the foraging success of spider by luring prey to the web. *Micrathena sexspinos* spiders on decorated webs intercepted significantly more bees than on empty frames and spiders on undecorated webs, which is in agreement with the hypothesis. The hypothesis has been partially supported among *Argiope* species; however, there is almost no support for other genera of araneids such as *Alloctoclosa* (Eberhard 2003), *Araneus* (Eberhard 2008, but see Bruce et al. 2001), *Cyclosa* (Baba 2003; Chou et al. 2005; Gonzaga & Vasconcellos-Neto 2005, but see Tso 1998b) and *Gasteracantha* (Jaffé et al. 2006; Eberhard 2006; Gawryszewski & Motta 2008). The same can be said for the uloborids *Philoponella* (Eberhard 2006) and *Zosis* (formerly *Uloborus*, Bruce et al. 2005; Eberhard 2006).

There is a large variation of decorations at the species and individual level within these genera (Herberstein et al. 2000); in marked difference, *Micrathena* only shows a monophormic linear decoration pattern (Scharff & Coddington 1997). This varies from the polymorphism of decoration patterns found, for example, in the model genus *Argiope* that might be related to several functions (e.g., Bruce & Herberstein 2005). The linear pattern is probably primitive for the araneids *Argiope*, *Cyclosa* and *Gasteracantha* (Herberstein et al. 2000; Cheng et al. 2010). In contrast, it appeared de novo in *Micrathena* (Herberstein et al. 2000). Therefore, the function of web decorations in *Micrathena* might differ from its function in other genera. The lability of this trait, evolving at least nine

times in 15 different genera, suggests the possibility of different functions (Scharff & Coddington 1997; Herberstein et al. 2000).

Multiple functions for decorations have almost no support in the literature, and *Micrathena sexspinos*'s decoration does not seem to be an exception. For instance, individuals are found in confined spaces (e.g., shrubs) and therefore it is very unlikely that the decoration acts as a web advertisement for birds (e.g., Blackledge & Wenzel 1999; Jaffé et al. 2006; Eberhard 2006; Gawryszewski & Motta 2008). Furthermore, the decoration probably does not work as a mechanical barrier against predators, because the spider never rests behind the decorations, a behavior found in *Argiope* species (e.g., Li et al. 2003). Moreover, the size and shape of the decoration does not provide full cover to the spider. *Micrathena sexspinos* generally builds its web in or between the vegetation; consequently, one side of the web is almost always unreachable to approaching predators (e.g., spider-hunting wasp). It seems that the main anti-predator response of *M. sexspinos* is to shuttle to the other side of the web through the central hole in the hub or dropping from the web (pers. obs.).

Micrathena sexspinos's decoration pattern does not appear to function for thermoregulation of the spider (Humphreys 1992). The decoration does not provide full shade against solar radiation, and the spider does not usually rest behind the decoration (pers. obs.). A mechanical function on the web also seems unlikely, since several individuals can be found near to each other on both decorated and undecorated webs under similar environmental conditions. If decorations were important for strengthening the web, then it is expected that spiders under similar environmental conditions would show similar decorating behaviors. However, I could not evaluate if an increase of the web tension occurs due to the decoration. For instance, *Octonoba sybotides* (Bösenberg & Strand 1906) build decorations that lure prey to the web (Watanabe 1999) and increase web tension (Watanabe 2000), which allows the spider to respond faster to small prey caught in the web. Therefore, these two functions are not necessarily mutually exclusive, and both increase foraging success of the spider.

Luring prey to the web might not depend entirely on the web decoration but perhaps on the spider coloration as well (e.g., *Argiope* spp., Craig & Ebert 1994; Tso et al. 2002; Cheng & Tso 2007; Bush et al. 2008). The lack of significant differences between undecorated webs and empty frames does not support the prey-attraction function of body coloration as suggested for other araneids. However, this study was not designed to evaluate the effect of spider morphology on prey behavior. In *Micrathena gracilis* (Walckenaer 1805), Vanderhoff et al. (2008) did not find any effect of spider presence on prey capture rate, nor did he find differences between control and black-painted spiders. Therefore, body coloration of *M.*

sexspinosa might serve for another function, for instance in camouflage of the spider (Hoese et al. 2006; Václav & Prokop 2006). Nevertheless, the best method for evaluating the effect of the spider (e.g., coloration) on prey attraction is by comparing webs with spiders against webs without spiders, a comparison I did not include in this study. In addition, the spectral measurements of the decorations, spiders and the background can be used to evaluate their visibility to prey in order to confirm the prey attraction function (e.g., Bruce et al. 2005).

The decorating behavior of *M. sexspinosa* could offer a great advantage for resource use; however, further research is needed in order to evaluate whether a disadvantage of building the decoration exists as in other decorating species (Bruce 2006, Herberstein et al. 2000).

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LITERATURE CITED

Baba, Y. 2003. Testing for the effect of detritus stabilimenta on foraging success in *Cyclosa octotuberculata* (Araneae: Araneidae). *Acta Arachnologica* 52:1-3.

Blackledge, T.A. & J.W. Wenzel. 1999. Do stabilimenta in orb webs attract prey or defend spiders? *Behavioral Ecology* 10:372-376.

Blackledge, T.A. & J.W. Wenzel. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* 138:155-171.

Bruce, M.J. 2006. Silk decorations: controversy and consensus. *Journal of Zoology* 269:89-97.

Bruce, M.J. & M.E. Herberstein. 2005. Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. *Journal of Natural History* 39:3833-3845.

Bruce, M.J., M.E. Herberstein & M.A. Elgar. 2001. Signalling conflict between predator and prey attraction. *Journal of Evolutionary Biology* 14:786-794.

Bruce, M.J., A.M. Heiling & M.E. Herberstein. 2004. Web decorations and foraging success in '*Araneus' eburnus* (Araneae: Araneidae). *Annales Zoologici Fennici* 41:563-575.

Bruce, M.J., A.M. Heiling & M.E. Herberstein. 2005. Spider signals: are web decorations visible to birds and bees? *Biology Letters* 1:299-302.

Bush, A.A., D.W. Yu & M.E. Herberstein. 2008. Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae). *Proceeding of the Royal Society B* 275:1337-1342.

Cheng, R.-C. & I.-M. Tso. 2007. Signaling by decorating webs: luring prey or deterring predators? *Behavioral Ecology* 18:1-7.

Cheng, R.-C., E.-C. Yang, C.-P. Lin, M.E. Herberstein & I.-M. Tso. 2010. Insect form vision as one potential shaping force of spider web decoration design. *Journal of Experimental Biology* 213:759-768.

Chou, I.-C., P.-H. Wan, P.-S. Shen & I.-M. Tso. 2005. A test of prey-attracting and predator defence functions of prey carcass decorations built by *Cyclosa* spiders. *Animal Behaviour* 69:1055-1061.

Craig, C.L. & G.D. Bernard. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* 71:616-623.

Craig, C.L. & K. Ebert. 1994. Colour and pattern in predator-prey interactions; the bright body colours and patterns of a tropical orbspinning spider attract flower-seeking prey. *Functional Ecology* 8:616-620.

Craig, C.L., S.G. Wolf, J.L.D. Davis, M.E. Hauber & J.L. Maas. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. *Evolution* 55:986-993.

Eberhard, W.G. 2003. Substitution of silk stabilimenta for egg sacs by *Alloctyclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. *Behaviour* 140:847-868.

Eberhard, W.G. 2006. Stabilimenta of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): evidence against a prey attractant function. *Biotropica* 39:216-220.

Eberhard, W.G. 2008. *Araneus expletus* (Araneae, Araneidae): another stabilimentum that does not function to attract prey. *Journal of Arachnology* 36:191-194.

Gálvez, D. 2009. Frame-web-choice experiments with stingless bees support the prey-attraction hypothesis for silk decorations in *Argiope savignyi*. *Journal of Arachnology* 37:249-253.

Gawryszewski, F.M. & P.C. Motta. 2008. The silk tuft web decorations of the orb-weaver *Gasteracantha cancriformis*: testing the prey attraction and the web advertisement hypotheses. *Behaviour* 145:277-295.

Gonzaga, M.O. & J. Vasconcellos-Neto. 2005. Testing the functions of detritus stabilimenta in webs of *Cyclosa fillineata* and *Cyclosa morretes* (Araneae: Araneidae): do they attract prey or reduce the risk of predation? *Ethology* 111:479-491.

Herberstein, M.E. 2000. Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? *Australian Journal of Zoology* 48:217-223.

Herberstein, M.E., C.L. Craig, J.A. Coddington & M.A. Elgar. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews* 75:649-669.

Hoese, F.J., E.A.J. Law, D. Rao & M.E. Herberstein. 2006. Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage? *Behaviour* 143:763-781.

Humphreys, W.F. 1992. Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behavior. *Bulletin of the British Arachnological Society* 9:47-52.

Jaffé, R., W.G. Eberhard, C.D. Angelo, D. Eusse, A. Gutierrez, S. Quijas, A. Rodriguez & M. Rodriguez. 2006. Caution, webs in the way! Possible functions of silk stabilimenta in *Gasteracantha cancriformis* (Araneae, Araneidae). *Journal of Arachnology* 34:448-455.

Levi, H.W. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetactis* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 150:429-618.

Li, D. 2005. Spiders that decorate their webs at higher frequency intercept more prey and grow faster. *Proceedings of the Royal Society B* 272:1753-1757.

Li, D. & M.L.M. Lim. 2005. Ultraviolet cues affect the foraging behaviour of jumping spiders. *Animal Behaviour* 70:771-776.

Li, D., L.M. Kok, W.K. Seah & M.L.M. Lim. 2003. Age-dependent stabilimentum-associated predator avoidance behaviours in orb-weaving spiders. *Behaviour* 140:1135-1152.

Li, D., M.L.M. Lim, W.K. Seah & S.L. Tay. 2004. Prey attraction as a possible function of discoid stabilimenta of juvenile orb-spinning spiders. *Animal Behaviour* 68:629-635.

McClintock, W.J. & G.N. Dodson. 1999. Notes on *Cyclosa insulana* (Araneae, Araneidae) of Papua New Guinea. *Journal of Arachnology* 27:685-688.

Nentwig, W. 1985. Top-asymmetry in vertical orbwebs: a functional explanation and attendant complications. *Oecologia* 67:111-112.

- Nentwig, W., B. Cutler & S. Heimer. 1993. Spiders of Panama: Biogeography, Investigation, Phenology, Checklist, Key, and Bibliography of a Tropical Spider Fauna. CRC Press, Boca Raton, Florida.
- R Development Core Team. 2009. R: a Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Online at <http://www.R-project.org>.
- Robinson, M.H. & B.C. Robinson. 1973. The stabilimentum of *Nephila clavipes* and the origins of stabilimentum-building in Araneids. *Psyche* 80:277–288.
- Sanford, R.L., P. Paaby, Jr., J.C. Luvall & E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pp. 19–33. *In* La Selva. Ecology and Natural History of a Neotropical Rainforest. (L.A. McDade, K.S. Bawa, H.A. Hespeneide & G.S. Hartshorn, eds.). University of Chicago Press, Chicago, Illinois.
- Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society* 120:355–424.
- Seah, W.K. & D. Li. 2001. Stabilimenta attract unwelcome predators to orb-webs. *Proceedings of the Royal Society of London B* 268:1553–1558.
- Tan, E.J. & D. Li. 2009. Detritus decorations of an orb-weaving spider, *Cyclosa muhneinensis* (Thorell): for food or camouflage? *Journal of Experimental Biology* 212:1832–1839.
- Tso, I.-M. 1998. Isolated spider web stabilimentum attracts insects. *Behaviour* 135:311–319.
- Tso, I.-M., P.L. Tai, T.H. Ku, C.H. Kuo & E.C. Yang. 2002. Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Animal Behavior* 63:175–182.
- Václav, R. & P. Prokop. 2006. Does the appearance of orb-weaving spiders attract prey? *Annales Zoologici Fennici* 43:65–71.
- Vanderhoff, E.N., C.J. Byers & C.J. Hanna. 2008. Do the color and pattern of *Micrathena gracilis* (Araneae: Araneidae) attract prey? Examination of the prey attraction hypothesis and crypsis. *Journal of Insect Behavior* 21:469–475.
- Walter, A., P. Bliss, M.A. Elgar & R.F.A. Moritz. 2008. *Argiope bruennichi* shows a drinking-like behaviour in web hub decorations (Araneae, Araneidae). *Journal of Ethology* 27:25–29.
- Watanabe, T. 1999. Prey attraction as a possible function of the decoration of the uloborid spider *Optonoba sybotides*. *Behavioral Ecology* 10:607–611.
- Watanabe, T. 2000. Web tuning of an orb-web spider, *Optonoba sybotides*, regulates prey-catching behaviour. *Proceedings of the Royal Society B* 267:565–569.

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